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A New Species of *Tsuga* (Pinaceae) based on Lignified Wood from the Late Miocene of Central Yunnan, China, and Its Paleoenvironmental Implications

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Abstract: A new species, *Tsuga nanfengensis* sp. nov. (Pinaceae), is described on the basis of lignified fossil wood from the late Miocene of the Xianfeng Basin, central Yunnan, southwestern China. Detailed observation of the fossil wood specimens show the following characteristics: distinct growth rings, absence of resin canals, uniseriate bordered pits in the radial wall of tracheids, ray tracheids and piceoid and cupressoid cross-field pits. These features indicate similarities to the wood of extant *Tsuga canadensis*, *T. chinensis*, and *T. dumosa*. According to the fossil record, *Tsuga* was present in Xundian County during the Miocene. Today *Tsuga* is drought intolerant, preferring wet conditions with no extant species growing naturally in Xundian County. The presence of *Tsuga* in the Miocene of Xundian County indicates a humid climate consistent with previous palaeoclimatic reconstructions showing a wetter and probably shorter dry season in the Miocene, relative to the present day. Therefore, the change in the local climate such as increasing aridity through the Miocene might explain the local extinction of *Tsuga* from central Yunnan.

Key words: *Tsuga*, fossil wood, palaeoclimate, late Miocene, Yunnan

1 Introduction

Tsuga (Endl.) Carr. (Hemlock), belonging to the family Pinaceae, is a key component of the subalpine and lowland humid mixed coniferous and broad-leaved forests (Horikawa, 1972; Farjon, 1990; Fu et al., 1999). Extant *Tsuga* grows in differing environments across a broad range of altitude and temperature but always in areas with a relatively humid climate where water stress is minimal (Farjon, 1990; Taylor, 1993; Yamazaki, 1995; Fu et al., 1999; Haas and McAndrews, 2000). Thus, as a drought-intolerant genus, *Tsuga* is usually considered to be a good indicator of humid conditions during the geological past (Wang, 1996; Fauquette et al., 1998; Nakagawa et al., 2002; Xu, 2002; LePage, 2003; Xu et al., 2004, 2008; Kou et al., 2006; Yang et al., 2009; Zhang et al., 2012). Up to twenty five extant species of *Tsuga* have been recognized, with eight to thirteen species generally accepted by different authors (Flous, 1936; Gaussen, 1966; Zheng, 1983; Silba, 1986; Farjon, 1990; Fu et al., 1999; Eckenwalder, 2009; Farjon, 2010). Currently, the most widely accepted classification of extant *Tsuga* is the classification of Farjon (1990, 2010) that consists of nine species: two occurring in western North America, two in eastern North America, two in Japan, and three in China and the Himalayas.

Since the Late Cretaceous, fossils of *Tsuga* in the forms of pollen, leaves, wood, seed cones and seeds, have been

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well-represented in North America and Eurasia (LePage, 2003). The oldest fossil record of *Tsuga* pollen was reported from the Late Cretaceous (ca. 90 Ma) of Poland (Macko, 1963). From the Eocene to the Pliocene, *Tsuga* pollen became widespread over Eurasia and North America (LePage, 2003). During the Pleistocene, *Tsuga* pollen is found in the mid-latitudinal regions of Eurasia and eastern North America, but has disappeared from the high latitudinal regions of Eurasia and western North America (LePage, 2003). The oldest *Tsuga* macrofossils are seeds discovered in the middle Eocene deposits of North America (ca. 48.7 Ma) (Currah et al., 1998). Fossil *Tsuga* wood finds are rare relative to the numerous records of *Tsuga* pollen, seed cones and seeds. In North America, fossil wood of *Tsuga* has been reported from the Pleistocene (Knowlton, 1894, 1895; Brown, 1935; Berry, 1952). In Eurasia, fossil wood records of *Tsuga* have been found in the Miocene of Japan (Watari, 1956; Jeong et al., 2012), and the Pliocene of Italy (Tongiorgi, 1936), Germany (Gottwald, 1981) and China (Yi et al., 2005), in addition to the Pleistocene of the Czech Republic (Opravil, 1959).

In China fossil pollen records indicate that *Tsuga* was widely distributed in northern and northeastern regions during the Cenozoic (Li, 1998; Wang, 1999; Sun and Wang, 2005; Yang et al., 2009). During the Paleogene, *Tsuga* species were widely distributed in northern and northeastern China to at least 48º N (Xia and Wang, 1987; Li, 1998). By the Miocene, pollen records indicate that *Tsuga* was abundant from northwestern across to eastern China (Wang, 1999; Sun and Wang, 2005). However, in southwestern China where one-third of extant *Tsuga* species occur, the fossil record of *Tsuga* is sparse. To date, the oldest *Tsuga* macrofossil recovered from this region was a piece of wood discovered in the late Pliocene deposits in Yunnan Province, southwestern China, which showed a close affinity to *T. dumosa* (Yi et al., 2005). More recently, a new fossil species, *Tsuga xianfengensis* Xing et Zhou, was described, based on two compressed cones originating from the late Miocene Xianfeng flora of Yunnan (Xing et al., 2013b). A few fossil cones have been reported from the late Pliocene Mula Formation, Sichuan Province in southwestern China (Chen et al., 1986).

In this paper, we report a new record of fossil wood which shows close affinity to *Tsuga* from the Upper Miocene Xiaolongtan Formation of central Yunnan, southwestern China. In addition, we discuss its palaeoenvironmental implications.

2 Materials and Methods

Fossil wood was collected from the Nanfeng coal-mine, Xianfeng Basin, Xundian County (Fig. 1; 25°29′41″ N 103°01′13″ E, 2200 m a.s.l.), located about 60 km north of Kunming, central Yunnan Province, southwestern China. The geology of this coal-mine has been discussed in several studies and the fossiliferous layers are assigned to the Xiaolongtan Formation (Fig. 2; Xing et al., 1999; Wu

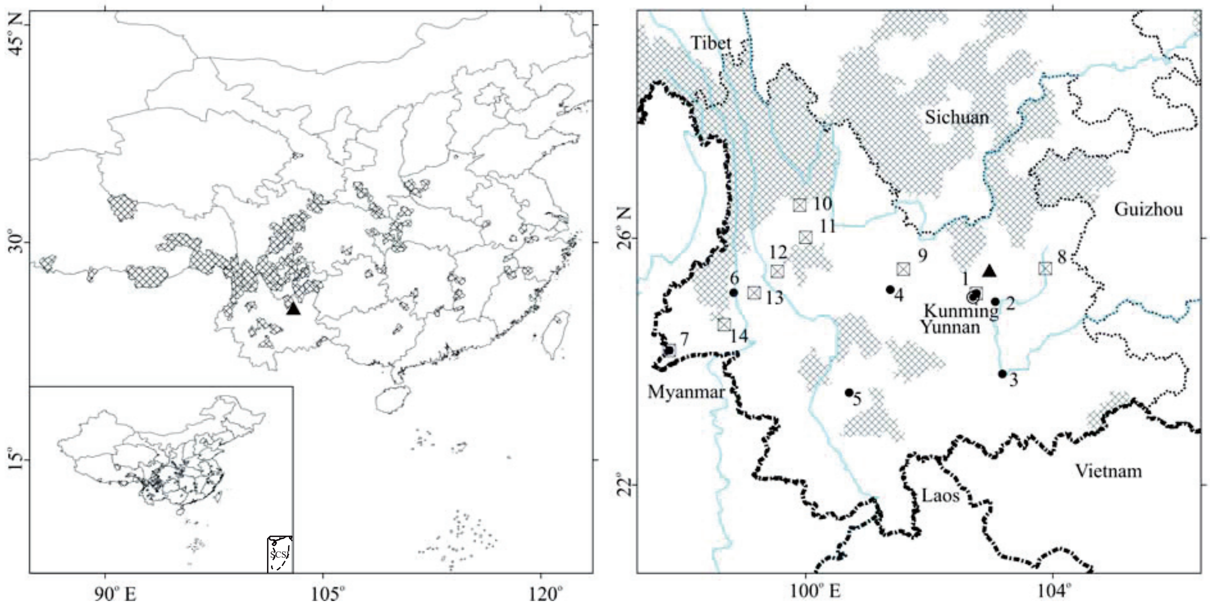

Fig. 1. Distribution of *Tsuga* in China (left) and fossil sites bearing *Tsuga* in Yunnan Province (right).

Nanfeng coal-mine is marked by a black triangle, distribution of extant *Tsuga* in China by diagonal grids, Miocene fossil sites in Yunnan containing *Tsuga* by dots, Pliocene sites by squares with cross. The fossil sites are: 1, Songhua Basin, Kunming City (Li and Wu, 1978); 2, Kebao coal-mine, Yiliang County (Li, 1981); 3, Xiaolongtan Basin, Kaiyuan County (Wang, 1996); 4, Lühe coal-mine, Chuxiong County (Xu et al., 2008); 5, Jinggu Basin (Lin et al., 2000); 6, Tengchong County (Tao and Du, 1982); 7, Longchuan Basin (Lin et al., 2000); 8, Qujing Basin (Wang and Shu, 2004); 9, Yuanmou Basin (Liu et al., 2002); 10, Jianchuan Basin (Tang and Hu, 1993); 11, Eryuan Basin (Tao and Kong, 1973); 12. Yongping Basin (Tang and Hu, 1993); 13, Yangyi coal-mine, Baoshan County (Xu, 2002); 14, Daba coal-mine, Longling County (Xu, 2002).

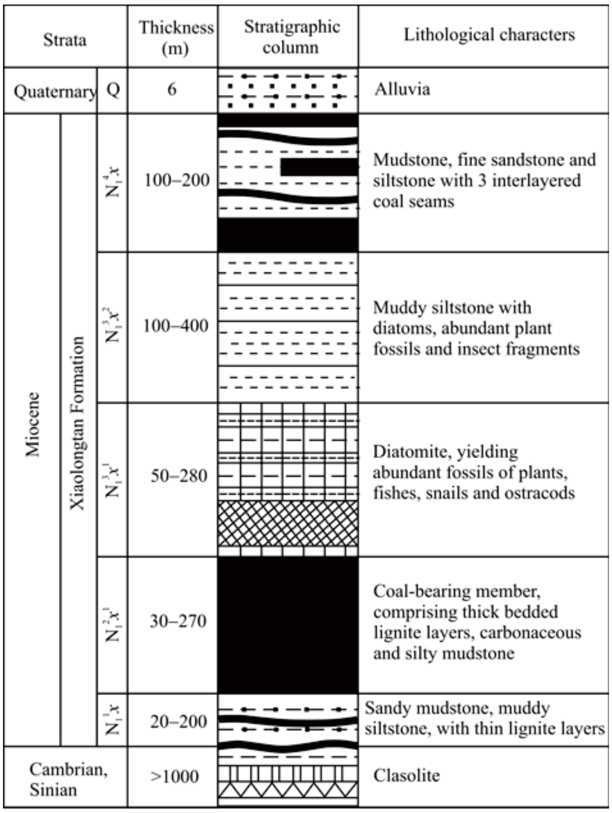

Fig. 2. Stratigraphy and lithology of the Nanfeng coal-mine (after Xing et al., 2010). The member from which the fossil wood was collected is marked by a star.

et al., 2006). The geological age of the Xiaolongtan Formation is considered to be late Miocene, based on mammal fossils such as *Tetralophodon xiaolongtanensis* Chow et Chang (Dong, 1987), plant macrofossils (e.g. *Quercus* L., Zhou, 1985, 2000; Xia et al, 2009) and pollen (e.g. *Compositoipollenites* Potonié, Wang, 1996). The lithological sequence of this formation comprises four members, namely N_1^1x–N_1^4x, the abundant plant macrofossils, bivalves, and insect fragments originate from the $N_1^3x^2$ member (Xing et al., 1999; Wu et al., 2006; Xing et al., 2010, 2012, 2013a, b). The fossil woods originate from the N_1^4x member (Fig. 2). The N_1^4x member is characterized by cyclical deposits of sandstone, siltstone and mudstone with coal seams. This type of deposit indicates the presence of marginal, occasionally deep, open lake environments periodically with swamp and flooding. The fossil wood was deposited ex situ and is likely to have been transported to the site of deposition by flowing water.

Eighteen samples of fossil wood were studied: they are lignified, dark brown in colour, in the size range of 1.5–25 × 4–26 cm in diameter and 11–78 cm in length, often compressed in transverse section. Thin sections were made following a technique described by Gammerman et al. (1946) for slightly lignified fossil woods. Each specimen was sectioned in three planes (transverse, radial longitudinal and tangential longitudinal) using a sliding microtome (Leica SM2010R). The optical examination and photomicrographs were undertaken using a digital imaging system (Leica DM750). The specimens were studied in detail using a scanning electron microscope (SEM, Zeiss EVO LS10); samples for SEM were prepared based on a technique described by Zhou and Jiang (1994). Anatomical terms used in this paper follow the recommendations of the IAWA List of microscopic features for softwood identification (IAWA Committee, 2004).

3 Systematic Description

Family PINACEAE M. Adanson, 1763

Genus ***Tsuga*** (Endlicher) Carrière, 1855

Species *Tsuga nanfengensis* O.V. Bondarenko, H.B. Wang et Z.K. Zhou sp. nov.

Figs. 3, 4

Holotype: NF 216, a specimen 15 × 18 cm in diameter and 42 cm long.

Material: nos. NF 028, 031, 035, 062, 065, 070, 093, 150, 165, 177, 187, 216 (holotype), 221, 242, 248, 250, 256, 301.

Repository: Laboratory of Palaeoecology, Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences, Mengla, Yunnan, China.

Locality: Nanfeng coal-mine, Xianfeng Township, Xundian County, central Yunnan Province, southwestern China.

Horizon: Xiaolongtan Formation.

Age: late Miocene.

Diagnosis: Growth rings distinct. Pits in the radial walls of tracheids uniseriate, circular and elliptical, 16–24 μm in diameter; pit apertures circular. Pits in the tangential walls of tracheids sparse, uniseriate, circular, 6–8 μm in diameter. Uniseriate rays 1–17 cells high, sometimes partially biseriate (1–3 layers). Both normal and traumatic resin canals absent. Piceoid and cupressoid cross-field pits, 1–4(6) per cross-field, 2–4 μm in diameter.

Description: Growth rings are distinct (Figs. 3a, b), frequently compressed in either the radial or tangential direction. Late wood occupies nearly 1/4–1/3 of the ring width (Fig. 3a). Transition from early (spring) wood to late (summer) wood is more or less gradual (Figs. 3a, b).

In the transverse section the early wood tracheids are thin-walled, rectangular, squarish, polygonal, and radially elongated; late wood tracheids are thick-walled and radially flattened (Figs. 3a, b). The tangential diameter of early wood tracheids measures 35–46 μm, with a mean

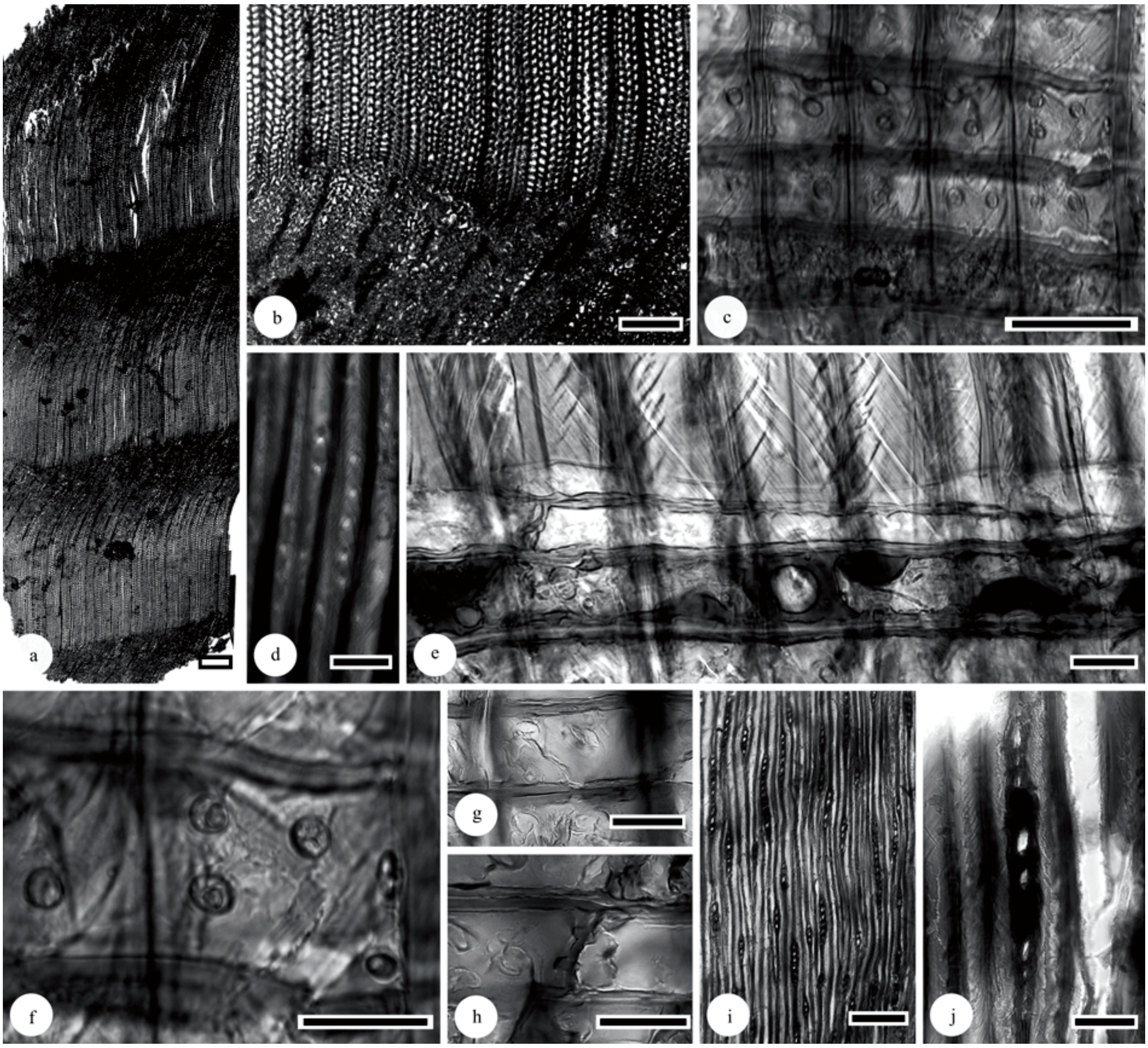

Fig. 3. *Tsuga nanfengensis* sp. nov. (NF 216), images were taken under a light microscope.

a, Overview of cross section showing growth rings and transition from earlywood to latewood. b, Cross section displaying distinct ring boundary. c, Radial section showing ray tracheids and cross-field pitting. d, Radial section displaying uniseriate pitting in radial walls of tracheids. e, Radial section showing ray tracheids in a single marginal row along the ray. f, Radial section showing cross-field pitting. g, Radial section displaying distinctly pitted horizontal walls of ray parenchyma cells. h, Radial section showing distinctly pitted (nodular) end walls of ray parenchyma cells and piceoid pits in the cross-field. i, Overview of tangential section displaying uniseriate rays. j, Tangential section showing a uniseriate ray. Scale bars: 500 μm (a), 200 μm (b, i), 50 μm (c, d, j), 20 μm (e, f, g, h).

and standard deviation (SD) of 41 ± 3 μm, and a radial diameter of 30–51 μm (44 ± 4 μm). The tangential diameter of late wood tracheids measures 22–37 μm (29 ± 5 μm), radial diameter is 16–33 μm (24 ± 3 μm). Thickness of early wood tracheid walls measures 2.0–2.6 μm, and late wood tracheids 3.5–4.8 μm. The bordered pits in the radial walls of early wood tracheids are uniseriate, circular, and elliptical, 16–24 μm in diameter (18 ± 2 μm); pit apertures are circular (Fig. 3d). The bordered pits in the radial walls of late wood tracheids are uniseriate, circular, 5-10 μm in diameter (8 ± 1 μm); pit apertures are lens-shaped. Torus is smooth and torus extensions sometimes occur on pit membranes (Fig. 4a). The bordered pits in the tangential walls of tracheids are sparse, uniseriate, circular, 6–8 μm in diameter. A warty layer is present on pit borders and surfaces of inner wall of tracheids; warts are uniform in size (Fig. 4e).

Axial parenchyma is marginal and sparse, distributed mainly in late wood. Axial parenchyma is observed only in the transverse sections in some growth rings but is not observed in either the radial or tangential sections.

Rays are uniseriate, sometimes partially biseriate (1–3 cell layers), 1–17 cells high (most frequently 4–12) (Figs. 3i, j), and consist of ray parenchyma cells and ray tracheids (Figs. 3c, e). Ray parenchyma cells are elliptical, circular and/or squarish, frequently with dark-coloured contents. The horizontal walls of ray parenchyma cells are thick and distinctly pitted; pits are sparse but distinct (Fig.

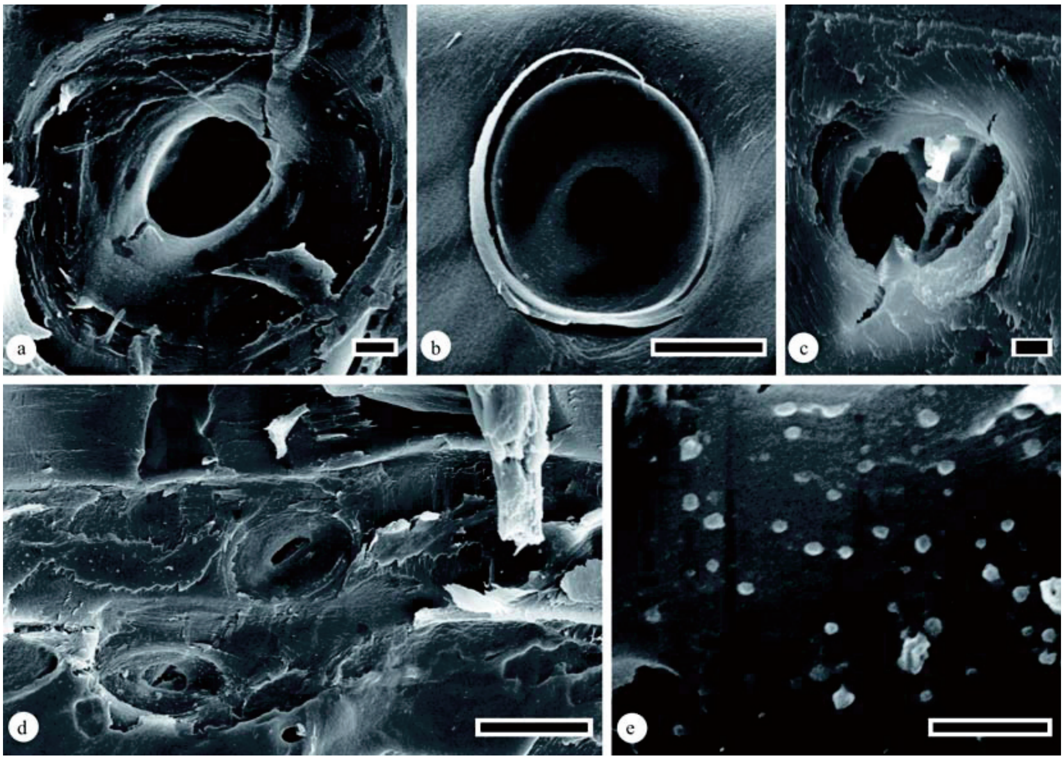

Fig. 4. *Tsuga nanfengensis* sp. nov. (NF 216) and modern *Tsuga* sp., images were taken under a scanning electron microscope.

a, Radial section showing pit in radial wall of tracheid with torus extension in studied fossil wood. b, Radial section displaying pit in radial wall of tracheid with torus extension in modern *Tsuga dumosa*. c, Radial section showing piceoid pit on cross-field. d, Radial section showing bordered pit in radial wall of ray tracheid. e, Radial section displaying warty layer of the secondary wall of tracheid. Scale bars: 10 μm (b, d), 2 μm (a, c, e).

3g). The end walls of ray parenchyma cells are distinctly pitted (nodular), with 2–5 nodules (Fig. 3h); indentures present. Ray tracheids form a single marginal row along the ray; internal cell walls of ray tracheids are smooth, external walls are wavy (Fig. 3e). Bordered pits are circular, 5–7 μm in diameter, occurring in the radial walls of ray tracheids (Fig. 4d).

Cross-fields exhibit 1–6, but mostly 2–4, piceoid and cupressoid pits, 2–4 μm in diameter, arranged in 1–2 horizontal rows (Figs. 3c, f, 4c).

Both normal and traumatic resin canals are absent (Figs. 3a, i).

4 Discussion

4.1 Comparison with extant woods

The fossil species *Tsuga nanfengensis* described here is characterized by distinct growth rings, absence of resin canals, uniseriate bordered pits in the radial tracheid walls, smooth tori, presence of torus extensions, marginal sparse axial parenchyma, ray tracheids with smooth walls, ray parenchyma cells with thick distinctly pitted horizontal walls and distinctly pitted (nodular) end walls, piceoid and cupressoid cross-field pits (Figs. 3, 4).

Cephalotaxaceae and Taxaceae (Cheng et al., 1992; Zhou and Jiang, 1994) can both be eliminated as candidate families, as they possess distinct helical thickenings, which are not found in the fossil wood. Axial parenchyma is a character abundant in Cephalotaxaceae, Cupressaceae, and most Podocarpaceae, but very rarely present in Araucariaceae, Phyllocladaceae, Sciadopityaceae and Taxaceae. Our fossil wood has marginal sparse axial parenchyma and therefore the families mentioned above can also be excluded. Moreover, our fossil species has only uniseriate pitting in the radial tracheid walls (Fig. 3d), whereas Araucariaceae is typically characterized by tri- or more seriate pitting, alternately arranged (Cheng et al., 1992; Zhou and Jiang, 1994). The combination of wood anatomical characters such as distinct growth rings, large thin-walled early wood tracheids of rectangular outline and radially elongated (in transverse section), abietoid pitting in the walls of tracheids and ray cells, marginal sparse axial parenchyma, heterogeneous rays (i.e. with ray tracheids), and small bordered pits several in number per cross-field, indicates the described fossil wood should be assigned to the Pinaceae (Phillips, 1948; Greguss, 1955; Chavchavadze, 1979; Esteban et al., 2004; Esteban and de Palacios, 2009).

As with our fossil wood several extant members of Pinaceae including *Abies* Mill., *Tsuga* (Endl.) Carr., *Cedrus* Mill., and *Pseudolarix* Gord. lack normal resin canals (Phillips, 1948; Greguss, 1955; Chavchavadze, 1979; Cheng et al., 1992; Zhou and Jiang, 1994; Esteban et al., 2004; Esteban and de Palacios, 2009). The presence of predominantly elliptical apertures of the circular pits in the radial walls of tracheids excludes *Pseudolarix* (Budkevich, 1961). A capacity to form vertical traumatic resin canals and the absence of normal resin canals is a feature of *Abies*, *Tsuga* and *Cedrus*. In *Cedrus*, vertical traumatic resin canals occur in addition to horizontal resin canals (Chrysler, 1915; Yatsenko Khmelevsky, 1954; Budkevich, 1961; Alexeeva, 1964; Chavchavadze, 1979; Esteban and de Palacios , 2009).

Pits in the radial tracheid walls are bordered, predominantly uniseriate, sometimes biseriate in *Abies* and *Tsuga*, whereas in *Cedrus* alternate (araucarioid) pitting occasionally occurs in the radial walls of early wood tracheids along with predominantly abietoid pitting (Phillips, 1948; Greguss, 1955; Budkevich, 1961; Chavchavadze, 1979; Esteban et al., 2002, 2004). Our fossil samples only have abietoid pitting in the radial walls (Fig. 3d).

The torus is smooth in *Abies* and *Tsuga*, whereas *Cedrus* is typically characterized by a scalloped or dentate torus (Phillips, 1948; Greguss, 1955; Budkevich, 1961; Chavchavadze, 1979; Esteban et al., 2002, 2004). The presence of smooth tori in our samples and the absence of traumatic resin canals, especially horizontal ones, and the occasionally alternate arrangement (araucarioid) of the pits in the radial walls of early wood tracheids eliminates *Cedrus*.

Torus extensions (Figs. 4a, b) occur regularly in *Tsuga* (Phillips, 1948; Greguss, 1955; Budkevich, 1961; Chavchavadze, 1979; Esteban et al., 2002, 2004) but can also be observed sporadically in *Abies* (Willebrand, 1995).

Ray tracheids in *Tsuga* only occur along ray margins, while in *Abies* ray tracheids are lacking (Phillips, 1948; Greguss, 1955; Budkevich, 1961; Chavchavadze, 1979; Esteban and de Palacios , 2009), and since they are present in the fossil materials (Figs. 3e, 4d), *Abies* can be eliminated.

Wood of extant species of *Tsuga* can be distinguished by the cross-field pit arrangement (Greguss, 1955, 1963; Budkevich, 1961; Esteban et al., 2002, 2004; Esteban and de Palacios, 2009; Jiang et al., 2010). *Tsuga longibracteata* W.C. Cheng (included in *T. forrestii* Downie according to Farjon, 2010) has cupressoid, piceoid, and taxodioid cross-field pits as well as exclusively uniseriate rays. The two Japanese species, *T. diversifolia* (Maxim.) Mast. and *T. sieboldii* Carr., are characterized by piceoid and taxodioid cross-field pits and very short (up to 8 cells) exclusively uniseriate rays. *Tsuga heterophylla* (Rafin.) Sarg. and *T. mertensiana* (Bong.) Carr. are characterized by predominantly piceoid cross-field pitting whereas *T. dumosa* (D. Don) Eichler and *T. chinensis* (Franch.) E. Pritzel exhibit cupressoid cross-field pitting. Moreover, the North-American species *T. heterophylla* and *T. mertensiana* are distinguished by their high rays (30-35 cells) and a smaller number of pits per cross-field (up to 4). *Tsuga canadensis* (L.) Carr. is only characterized by the presence of both cupressoid and piceoid cross-field pitting. Since the fossil material has cupressoid and piceoid cross-field pits, it is similar to those species having cupressoid and/or piceoid cross-field pits: *T. canadensis*, *T. chinensis*, *T. dumosa*, *T. heterophylla*, and *T. mertensiana* (Table 1). However, our fossils have short rays (up to 17 cells) and up to six pits on a cross-field, so we can exclude *T. heterophylla* and *T. mertensiana* from possible affinities, leaving the closest anatomical similarity to that of the wood of *T. canadensis*, *T. chinensis* and *T. dumosa*.

4.2 Comparison with fossil woods

As mentioned above, fossil wood of *Tsuga* is less common than other organs. Moreover, some fossil woods such as *Tsuga chiarugii* Tongiorgi from the Pliocene of Italy (Tongiorgi, 1936), *T. mertensiana* (Knowlton, 1894, 1895) and *T. canadensis* (Brown, 1935) from the Pleistocene of North America, and *Tsuga* sp. from the Pleistocene of the Czech Republic (Opravil, 1959) and the middle Pleistocene of Japan (Noshiro et al., 1987), are mentioned either with no wood anatomical description or with a very short description that does not allow any meaningful comparison between the fossil wood studied here and those previously reported.

Fossil wood of *Tsuga longibracteata* from the Neogene of China described by Chen et al. (1992) can be differentiated from the fossil material described here by normal vertical resin canals typical of *Keteleeria* wood. Later, Qi et al. (2005) considered *Tsuga longibracteata* as *Tsugo-keteleeria longibracteata* (W.C. Cheng) Campo-Duplan et Gaussen. According to Ho (1949), Yu (1956) and Budkevich (1961), the extant *T. longibracteata* is characterized by the absence of resin canals (both normal and traumatic) although Jiang et al. (2010) reported the presence of traumatic ones.

At present, there are five well-described fossil wood taxa with affinities to *Tsuga*: *Tsugoxylon primaevum* Vozenin-Serra et Salard-Cheboldaeff from the Permo-Triassic of New Caledonia (Vozenin-Serra and Salard-Cheboldaeff, 1992), *Tsuga europliocaenum* Gottwald from the Pliocene of Germany (Gottwald, 1981), *Tsuga* sp. from the Miocene of Japan (Watari, 1956), *T. watariae* Jeong et Kim from the middle Miocene of Japan (Jeong et al., 2012), and *T.* cf. *dumosa* Eichler from the late Pliocene of China (Yi et al., 2005). However, all these fossil species differ distinctly from the present fossil wood by the presence of biseriate pits in the radial walls of the tracheids and in the type of cross-field pitting (Table 1). *Tsugoxylon primaevum* and *Tsuga europliocaenum* are distinct by having only piceoid cross-field pitting. *Tsuga watariae* is characterized by having only cupressoid cross field pitting whilst *T.* cf. *dumosa* has both cupressoid and taxodioid cross-field pitting.

Vozenin-Serra and Salard-Cheboldaeff (1992) established the genus *Tsugoxylon* for fossil wood that displays anatomical characters of the extant genus *Tsuga*. However, as previously noted, the wood described here shows no close resemblance to any of the known fossil woods of *Tsugoxylon*. Taking into consideration the fact that the fossil wood in the current study possesses the characteristic features seen in the wood of extant *Tsuga*, coupled with the recommendations of Yatsenko Khmelevsky (1954) and the Melbourne Code (McNeill, 2012) that state the use of fossil generic names should not be used if identification of a given fossil wood to a particular modern genus is possible, we believe that the application of the generic name *Tsugoxylon* is inappropriate. Therefore, the wood under this study is described as a new species, namely *Tsuga nanfengensis* sp. nov., taking particular note of the similarity between the wood of

Table 1 Comparative wood anatomy of *Tsuga nanfengensis* sp. nov. to living and fossil *Tsuga* species

Species	Distribution	Anatomical character									References
		Traumatic resin canals	Pits in radial wall of tracheids			Rays		Cross-field pitting			
			1-seriate	2-seriate	Diameter (μm)	Height (cells)	2-seriate rays	Number	Diameter (μm)	Type	
Tsuga nanfengensis sp. nov.	Yunnan, southwestern China; Late Miocene	?	++	?	16–24	1–17	+ ?	1–4(6)	2–4	piceoid, cupressoid	This paper
T. dumosa (D. Don) Eichler	Himalayan region	?	++	+ ?	10–14	1–25	+ ?	1–4(6)	5–6	cupressoid	Jiang et al. (2010)
T. chinensis (Franch.) E. Pritzel	South China	?	++	+ ?	12–16	1–25	?	1–3(6)	4–5	cupressoid	Jiang et al. (2010)
T. forrestii Downie	Southwestern China	?	+	+	16–18	1–17	?	1–4(6)	6–9	piceoid, cupressoid, taxodioid	Jiang et al. (2010)
T. sieboldii Carr.	South Japan	?	++	+ ?	16–18	2–8	?	1–4(5)	?	piceoid, taxodioid	Budkevich (1961); Greguss (1955, 1963)
T. diversifolia (Maxim.) Mast.	North Japan	?	+	?	13–17	1–6(12)	+ ?	3–4(8)	2–6	piceoid, taxodioid	Greguss (1955, 1963)
T. heterophylla (Rafin.) Sarg.	West North America	+	++	+ ?	12–15	1–15(30)	+	1–3(4)	4–6	piceoid	Budkevich (1961); Greguss (1955, 1963)
T. caroliniana Engelm.	East North America	?	?	?	?	?	?	?	?	?	
T. canadensis (L.) Carr.	East North America	?	++	+ ?	14–16	1–20	+ ?	1–4(7)	2–5	piceoid, cupressoid	Budkevich (1961); Greguss (1955, 1963)
T. mertensiana (Bong.) Carr.	West North America	+	++	+ ?	14–16	1–35	+ ?	1–4	?	piceoid	Greguss (1955, 1963)
Tsugoxylon primaevum Vozenin-Serra et Salard-Cheboldaeff (fossil)	New Caledonia; Permo-Triassic	?	+	+	11–12	1–15	?	1–5	6–7	piceoid	Vozenin-Serra & Salard-Cheboldaeff (1992)
Tsuga europlicaenum Gottwald (fossil)	Germany; Pliocene	?	+	+ ?	?	2–13	+ ?	2–5	5	piceoid	Gottwald (1981)
Tsuga sp. (fossil)	Japan; Miocene	?	+	+	15–20	1–18	?	2–4	?	cupressoid	Watari (1956)
T. watariae Jeong et Kim (fossil)	Japan; Middle Miocene	+	+	+	18	1–13	?	2–5	?	cupressoid	Jeong et al. (2012)
T. cf. *dumosa* (fossil)	China; Late Pliocene	?	++	+ ?	16–22	1–19	+ ?	1–5	?	cupressoid, taxodioid	Yi et al. (2005)

Note: (+) present, (?) absent, (++) frequent, (+ ?) rare, (?) no data.

extant *Tsuga canadensis*, *T. chinensis*, and *T. dumosa*.

4.3 Paleoenvironmental implications

The Nanfeng coal-mine yielded fossil woods with a low taxonomic diversity (*Abies* Mill., *Pinus* L., *Tsuga* and *Prunus* L.; 535 pieces of wood have been checked in total). These fossil materials can shed some light on the palaeoenvironment of central Yunnan during the Miocene. *Tsuga* is no longer present in Xundian County (Fig. 1), where the Nanfeng coal-mine is situated, which may be due to a change in the local environment.

Distinct growth rings (Figs. 3a, b) are characteristic of all the fossil woods of *Tsuga* studied here, providing evidence of a pronounced seasonality of climate. According to Creber and Chaloner (1984), the fossil woods are characterized by growth rings of type "B" (Fig. 3a), i.e. growth rings with a more or less gradual transition from early wood to late wood and a wide band of late wood that indicates a long growing season with an adequate water supply.

Extant *Tsuga* species are shade tolerant yet cannot tolerate long periods of drought (Farjon, 1990; Taylor, 1993; Yamazaki, 1995; Fu et al., 1999; Haas and McAndrews, 2000). In North America, 90% of *Tsuga* grow under a climate characterized by a mean annual precipitation (MAP) higher than 800 mm and a Moisture Index of 0.91 (Thompson et al., 1999). In the East Asian Monsoon region, *Tsuga* requires a MAP of at least 720 mm and a precipitation higher than 600 mm during the growing season (Yang et al., 2009). The present mean annual temperature (MAT) of the fossil locality is within the MAT range of the modern distribution of *Tsuga*; therefore, precipitation is probably the most important factor causing the disappearance of *Tsuga* in central Yunnan.

The most closely related extant species to the fossils in anatomical terms, *Tsuga canadensis*, *T. chinensis*, and *T. dumosa*, require MAP values of 710–1560 mm, 1096–1864 mm and 635–1489 mm respectively (Utescher and Mosbrugger, 1997–2013; Thompson et al., 1999; Yang et al., 2009).

At present, quantitative reconstructions of the late Miocene climate for the Lühe (Xu et al., 2008), Xiaolongtan (Xia et al., 2009), Lincang (Jacques et al., 2011a, b), and Xianfeng (Xing et al., 2012) coal-mines in Yunnan all show the late Miocene climate in Yunnan was a little warmer (i.e. ca. 1–5°C higher, MAT, Xing et al., 2012) and much wetter (i.e. ca. 100–500 mm higher, MAP, Xing et al., 2012), especially during the dry season, when compared with the present day. Based on the coexistence approach analysis with a leaf flora from the Xianfeng Basin, central Yunnan, southwestern China, Xing et al. (2012) demonstrated that the late Miocene climate in Xianfeng was clearly seasonal, slightly warmer, and significantly wetter than today. The analysis estimated a MAP of 794.7 mm for the three wettest months (MP3WET), and 248.0 mm for the three driest months (MP3DRY), unlike the present-day climate of Xianfeng with MP3WET of 584.5 mm and MP3DRY of 38.2 mm. Since the Xianfeng and Nanfeng coal-mines are only 3 km apart and both floras from these coal-mines are from the same stratigraphic level, it seems reasonable that the climate that occurred at the Xianfeng coal-mine also existed at the site of the Nanfeng coal-mine.

In all, the discovery of *Tsuga* fossil wood indicates a much wetter climate in central Yunnan during the late Miocene and presupposes higher precipitation during the dry season, which was of shorter duration than at present. The subsequent reduction and disjunction of the distributional area of *Tsuga* in Yunnan since the late Miocene are likely to have been caused by an increase in the aridity of the climate, monsoon intensity, and precipitation seasonality. Being similar to the distributional history of *Lindera* (Dao et al., 2013), as well as that of *Cedrus* in Yunnan (Su et al., 2013), the disappearance of *Tsuga* further underscores how the gradual aridification since the Neogene may have played an important role in shaping the current spatial vegetation pattern in Yunnan Province.

5 Conclusions

A comparison of extant wood with the anatomical features of the fossil material indicates that the closest living relatives are *Tsuga canadensis*, *T. chinensis* and *T. dumosa*. To date fossil wood of *Tsuga* is rare with only five well-described fossil wood taxa with affinities to *Tsuga*, but all of them differing from the fossil wood described in the present paper.

Quantitative reconstructions show that the late Miocene climate in Yunnan was a little warmer and much wetter than at present, a fact supported by the presence of *Tsuga* in the Nanfeng coal-mine. With subsequent (local) climate change, *Tsuga* was unable to continue growing in Xundian County.

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